AVIAN CONSERVATION IN A CHANGING ENVIRONMENT: SPECIES' RESPONSES AND THE EFFICIENCY OF CONSERVATION MEASURES

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Table of contributions

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Abstract

Human induced climate change will affect global biodiversity considerably. One of the most studied consequences is climate driven redistributions of species. Simultaneously, increasing land development resulting in habitat loss will add difficulties for species to adapt and redistribute under changing climate. Failing to move or adapt, species face a risk of extinction. The high latitude and high altitude species are facing increased risk of extinction because these species have limited possibilities to retreat and the warming has been faster in northern high latitudes than other regions

Protected areas are likely to aid species in adapting to the changing climate by preserving high quality natural habitats where species can thrive. However, due to extensive land use and habitat degradation protection cannot always cover a sufficient amount of high quality habitat. In this case, habitat restoration can be the solution to improve habitat quality and availability, which can have positive effects on the ability of species to move and persist under climate change.

The aim of this thesis is to shed light on how protected areas have been able to mitigate the negative effects of the current climate change. In addition, it studies the role of habitat quality in the processes of redistribution events. Lastly, the thesis evaluates how habitat enhancement by restoration affects the abundances of species threatened by wide-scale habitat loss and degradation. The focal species of the thesis are birds, owing to the extensive, long-term Finnish monitoring data which are unique even in a global perspective.

In the first chapter, I study changes in abundance of the past five decades on the trailing range edge of northern and leading range edge of southern bird species. This study shows that protected areas help northern bird species maintain their abundances on the southern boundary of their current area of distribution, while aiding certain southern bird species spread to new territories on the northern boundary of their distribution area. This suggests that protected areas are able to slow down the northbound retreat of species, but also facilitate northward range expansions of southern species.

The second chapter studies if the effect of conservation in mitigating climate driven changes observed in the first chapter increases with increasing coverage of the protected area network. The results show that in northern and central Finland the increasing protected area coverage in the landscape is indeed associated with communities that are more stable and less affected by climate driven changes. However, such effect was not found in southern Finland, where the protected area coverage was very low, and in fact could be too low to support detectable levels of community resilience against climate change.

Populations and communities are shown to be more resilient to environmental changes when higher proportions of suitable high-quality habitat is available. Thus habitat quality could certainly explain the results gained in chapters I & II. The chapter III studies the effect of habitat quality on the occurrence of the white-backed woodpecker. Woodpeckers occupied more frequently the high-

quality habitat patches than lower quality patches suggesting that colonization events are more and local extinctions less frequent on these sites. Thus, high-quality habitats seem to enhance the ability of species to move and persist and therefore, protection of these sites should be a priority under the redistributing outcome of climate change.

Chapter IV shows that habitat quality can be further improved through restoration. Counteracting the overgrowth of wetlands rapidly increased the number of staging and breeding birds. Many waterbird species are threatened and declining due to eutrophication and overgrowth and the results show that wetland management can mitigate these negative developments.

The thesis concludes that protecting high-quality habitats can mitigate climate change driven range and community changes. However, current trajectories of conservation seem to be inadequate to preserve the current biodiversity. Therefore, to meet the aims to prevent further biodiversity loss, extensive and rapid efforts to increase protected area coverage and connectivity are direly needed. The main conclusion of this thesis support these acts and the benefits this will have for preserving biodiversity in the future.

Tiivistelmä

Ilmastomuutoksella on todettu olevan huomattava vaikutus elinkirjoon. Sen tunnetuimpia seurauksia ovat levinneisyysaluemuutokset. Samanaikainen elinympäristöjen heikentyminen ja pirstoutuminen hankaloittaa lajien sopeutumista muuttuvaan ilmastoon. Mikäli lajit eivät pysty sopeutumaan tai siirtymään, niiden riski kuolla sukupuuttoon kasvaa. Etenkin pohjoiset lajit ovat vaarassa, sillä lämpeneminen on ollut nopeinta boreaalisella ja arktisella vyöhykkeellä ja näillä alueilla siirtymismahdollisuuksia rajoittavat jääMeri sekä kölivuoristo.

Suojelualueiden on oletettu auttavan sopeutumaan ilmastonmuutokseen säilyttämällä korkealaatuisia elinympäristöjä, joissa lajit voivat menestyä. Laaja-alaisen elinympäristöjen laadun heikkenemisen vuoksi suojelu ei pysty välttämättä turvaamaan kohtuullista määrää korkealaatuisia elinympäristöjä. Tällöin elinympäristöjen kunnostaminen voi luoda lisää korkealaatuisia ympäristöjä, mikä voi puolestaan parantaa lajien kykyä siirtyä ja sopeutua.

Väitöskirjani tarkoitus on tutkia ovatko suojelualueet kyenneet lieventämään ilmastomuutoksen epäedullisia vaikutuksia elinkirjoon. Tutkin, miten elinympäristön laatu vaikuttaa ilmastosta johtuviin levinneisyysaluemuutoksiin sekä onko kunnostuksella vaikutusta elinympäristöjen heikkenemisestä kärsivien lajien yksilömääriin. Väitöskirjani kohdelajeja ovat linnut, sillä suomalainen laaja ja pitkäjänteinen linnustonseuranta tarjoaa maailmanlaajuisesti ainutlaatuisen aineiston tutkia edellä mainittuja luonnon tapahtumaketjuja.

Ensimmäisessä osatyössä tutkin viimeisen viiden vuosikymmenen aikana tapahtuneita runsausmuutoksia lintulajien levinneisyysalueiden reunoilla. Verrattuna suojelemattomiin alueisiin, suojelualueilla pohjoiset lintulajit säilyivät runsaampina levinneisyytensä eteläreunalla. Vastaavasti osa eteläisistä lajeista runsastui suojelualueilla enemmän kuin suojelemattomilla levinneisyysalueen pohjoisreunalla. Suojelualueet vaikuttavat hidastavan pohjoisten lajien vetäytymistä, mutta myös auttavan eteläisiä lajeja levittäytymään kohti pohjoista.

Toisessa osatyössä tutkin, voimistuuko suojelualueiden ilmastovaikutusten ehkäisy suojelualueverkoston kattavuuden kasvaessa. Pohjois- ja Keski-Suomessa kattavampi suojelualueverkosto oli yhteydessä kasvaneeseen kykyyn puskuroida ilmastosta johtuvia lintuyhteisömuutoksia. Vastaavaa yhteyttä ei kuitenkaan havaittu Etelä-Suomessa, jossa suojelualueiden kattavuus oli hyvin alhainen, ja voi hyvinkin olla liian alhainen osoittaakseen merkittävää sietokykyä ilmastosta johtuvia yhteisömuutoksia vastaan.

Lajien kestokyvyn ympäristömuutoksia vastaan on osoitettu kasvavan korkealaatuisten elinympäristöjen saatavuuden parantuessa. Siksi elinympäristön laatu voisi selittää havaitut suojelualueiden myönteiset vaikutukset. Tutkin tätä kolmannessa osatyössä valkoselkätikan osalta. Tikkojen havaitsemistodennäköisyys oli huomattavasti suurempi korkealaatuisissa kuin huonompilaatuisissa elinympäristöissä. Tulokset viittaavat siihen, että tikat asuttivat korkealaatuiset elinympäristöt huonompilaatuisia useammin ja vastaavasti hylkäsivät ne huonompilaatuisia

harvemmin. Elinympäristön korkea laatu vaikuttaa siten parantavan tikkojen mahdollisuuksia siirtyä ja säilyä, ja näiden suojelun tulisi olla etusijalla ilmastonmuutoksen haittavaikutuksia torjuttaessa.

Neljäs osatyö osoittaa, että elinympäristön laatua voidaan parantaa kunnostamalla. Kosteikkojen umpeenkasvun torjuminen kasvatti lintujen määriä nopeasti. Rehevöityminen ja umpeenkasvu uhkaavat monia vesilintuja, ja kosteikkojen kunnostuksella uhkaa voidaan torjua.

Väitöskirjan johtopäätös on, että suojelemalla ja kunnostamalla korkealaatuisia elinympäristöjä voidaan lieventää ilmastomuutoksen aiheuttamia levinneisyysalue- ja yhteisömuutoksia. Nykyinen suojelutoimien laajuus on osoittautunut riittämättömäksi tavoitteessa ehkäistä elinkirjon väheneminen. Siksi tämän tavoitteen saavuttamiseksi tarvitaan laajoja ja nopeita toimia suojelualueverkoston kattavuuden ja kytkeytyneisyyden kasvattamiseksi. Väitöskirjani tulokset tukevat näitä toimia sekä niiden mukanaan tuomia hyötyjä elonkirjon säilyttämiseksi seuraaville sukupolville.

SUMMARY

1. Introduction

1.1 Anthropogenic changes in climate and environment

Anthropogenic climate change is projected to have a substantial effect on global biodiversity (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012) and none of our ecosystems remain unaffected (Scheffers et al., 2016). The warming climate is shifting isotherms towards higher latitudes and altitudes causing species to follow their climatic preferences which is projected to alter species occurrences markedly throughout the biota (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Thomas et al., 2004; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005). Already during the 21st century, the ranges of bird species are projected to change massively (Huntley, Collingham, Willis, & Green, 2008; Huntley, Green, Collingham, & Willis, 2007), leading to marked turnover in species composition and functional rearrangements within ecosystems (Lawler et al., 2009; Thuiller et al., 2014; Virkkala & Lehikoinen, 2017).

Other anthropogenic changes, including land use driven habitat loss and fragmentation are likely to hamper possibilities of species to follow their climatic envelopes (Collingham & Huntley, 2000; Higgins, Lavorel, & Revilla, 2003; Robillard, Coristine, Soares, & Kerr, 2015). Indeed, habitat availability and climate, together rather than separate, are best predictors of range shifts (Platts et al., 2019). This concurrent action of climate change and habitat destruction is projected to be disastrous for biodiversity (Oliver et al., 2017; Travis, 2003) and is likely to lead to increased extinction debt (Jackson & Sax, 2010). A rapidly changing climate adds difficulties to species already suffering from stressors such as habitat loss, diseases and/or competition of non-native or invasive species (Benning, LaPointe, Atkinson, & Vitousek, 2002; Parmesan, 2006). Habitat specialists, the occurrence of which is usually limited by habitat availability, are less able to shift their ranges under climate change than habitat generalists (Platts et al., 2019), a fact that further underlines the detrimental effects of habitat loss and climate change.

Boreal and arctic species may be of particular concern under these changes, because the northern high latitudes are warming at a higher velocity than other regions (IPCC, 2013, 2018) and therefore climate change-driven range shifts are expected to be the most pronounced at northern latitudes (Jetz, Wilcove, & Dobson, 2007). In a changing environment species have basically three options: i) adapt, ii) move or iii) perish (Davis, Shaw, & Etterson, 2005). The risk of the third option is ever increasing because species need to adapt to new climatic conditions at a remarkable pace and under stress. The risk of perishing is especially pronounced for high latitude and high altitude species since they have limited possibilities to retreat and thus are more likely to be trapped into climate sinks (Burrows et al., 2014; Pacifici et al., 2017). There is already evidence supporting this in Fennoscandia where northern bird species have also gone through severe declines in populations and shifted their distributions faster in contrary to southern birds (Lehikoinen, Green, Husby,

Kålås, & Lindström, 2014; Post et al., 2009; Virkkala & Lehikoinen, 2014). Therefore, arctic and boreal bird species are projected to undergo substantial range reductions under warming climate (Virkkala, Heikkinen, Leikola, & Luoto, 2008).

1.2 The role of protected areas under climate change

Protected areas are the cornerstones of nature conservation ensuring species and habitat existence (Watson, Dudley, Segan, & Hockings, 2014). By preserving high quality natural habitats, protected areas are likely to aid species in adapting to a changing climate by providing sources of colonizers and locations for new colonization. However, their performance in mitigating the impacts of climate change has been questioned (Ferro, Lemes, Melo, & Loyola, 2014; Monzón, Moyer-Horner, & Palamar, 2011). The questions raised concentrate on how well the static network of protected areas is able to preserve nature and ensure species persistence under the dynamic and asymmetrical process of climate change (Monzón et al., 2011). This may cause species to end up outside protected area networks when shifting their distributions in response to the climate (Araújo, Cabeza, Thuiller, Hannah, & Williams, 2004; Hannah et al., 2007). This in turn may lead to the troublesome situation where protected area networks no longer protect the species they were originally established for (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Coetzee, Robertson, Erasmus, Van Rensburg, & Thuiller, 2009; Hole et al., 2009). However, evidence suggests that protected areas are able to protect both endangered species and biodiversity from some of the detrimental effects of climate change (Thomas & Gillingham, 2015). This is remarkable since the detrimental effects of climate change are shown to have a more marked impact on species that are already of conservation concern (Massimino, Johnston, Gillings, Jiguet, & Pearce-Higgins, 2017). Other positive associations of protected areas in mitigating the negative effects of climate change include prevention of species retractions on the trailing range edges (Gillingham, Bradbury, et al., 2015) and the facilitation of distribution expansions (Thomas et al., 2012), and this ability can be increased by managing protected areas (Lawson, Bennie, Thomas, Hodgson, & Wilson, 2014).

1.3 Habitat management and restoration

Sometimes, due to extensive land use and habitat degradation, protection cannot cover a sufficient amount of high quality habitat. Then restoration may become essential for reaching the targets of species conservation (De Groot et al., 2013). Restoring degraded habitats and extending protected area networks to improve habitat connectivity are fundamental for conservation plans that aim to facilitate adaptation to climate change (Gillson, Dawson, Jack, & McGeoch, 2013; Mawdsley, O'Malley, & Ojima, 2009; Reside, Butt, & Adams, 2018; Shoo et al., 2013). Improvements in habitat quality and availability can considerably aid species movement and their ability to persist

under climate and/or other environmental changes (Hodgson, Thomas, et al., 2011).

Wetlands, even if protected, are susceptible to external threats deriving from the upper catchment area and may demand restoration in order to sustain their quality for inhabiting organisms (Ma, Cai, Li, & Chen, 2010). Moreover, habitat loss has had a major impact on wetlands, leading to more than half of the world's wetlands being lost during the last century (Davidson, 2014). Simultaneously, the remaining wetlands have been widely degraded (Ma et al., 2010) and indeed, degradation of fresh water bodies is recognized as one of the major threats to global biodiversity (Leadley et al., 2010). Anthropogenic nutrient runoff, resulting in hyper eutrophication is a central driver of wetland habitat degradation (Downing, 2014; Fraser & Keddy, 2005). This detrimental process is further intensified by climate change through increases in soil temperature, precipitation and meltwater from glaciers (Moss et al., 2011).

The combined effects of climate change driven threats and hyper eutrophication on wetlands are likely to substantially impact the distributions and abundancies of avian populations inhabiting these important habitats (Guillemain et al., 2013; Steen, Skagen, & Noon, 2014; Steen, Skagen, & Melcher, 2016). Symptoms of hyper-eutrophication are overgrowth and increased water turbidity (Ekholm & Mitikka, 2006; Moss et al., 2011; Zhao et al., 2015). These, in turn, reduce the abundancies of submerged vegetation and invertebrates that are essential food resources for waterbirds (Hansson, Bronmark, Nilsson, & Abjornsson, 2005; Hansson et al., 2010). Hyper-eutrophication also increases the number of cyprinid fish in wetlands leading to increased food competition between waterbirds and fish (Haas et al., 2007).

Hyper-eutrophication of wetlands in northern Europe has been associated with declining waterbird populations (Fox et al., 2016; Lehikoinen, Rintala, Lammi, & Poysa, 2016). However, a variety of wetland management and restoration actions have shown promise in enhancing conditions for waterbird communities (Bregnballe, Amstrup, Holm, Clausen, & Fox, 2014; Clausen, Stjernholm, & Clausen, 2013; Giles, 1994; Gleason, Euliss Jr., Tangen, Laubhan, & Browne, 2011; Holm & Clausen, 2006; Ma et al., 2010). Nevertheless, evidence-based knowledge regarding the effects of wetland management remains scarce (Mérő, Lontay, & Lengyel, 2015; Zedler, 2000).

2. Aims and outline of the thesis

Understanding the ecological, physiological, genetic and biogeographical mechanisms underpinning species range shifts is fundamental for designing effective conservation strategies and adaptations to climate change (Bonebrake et al., 2018).The role of protected areas under climate change has mainly been studied by modelling future projections of species distributions and assessing the climatic suitability of the projected new geographic region inhabited by the species (Araújo et al., 2011; Hannah et al., 2007; Hole et al., 2009). Bioclimatic envelope models have been the backbone of studies assessing the impact of climate change on biodiversity and species composition alterations, and also served as important tools in assessing the strengths and weaknesses of current protected area networks (e.g. (Araújo & Peterson, 2012; Heikkinen et al., 2006). Because of the usefulness of these tools, many studies have concentrated on projecting future impacts of climate change. However, there is a demand for more knowledge on the current and already manifested impacts of climate change. Such knowledge can be used not only for understanding the procession of climate change and the resulting impacts on the natural world, but also for validating and improving the aforementioned projections of future impacts (Pacifici et al., 2017). Moreover, most studies concerning species distribution changes under climate change are based on occurrence data, despite recent evidence showing that in fact abundance data yields higher reliability when generating outcomes for conservation prioritization (Howard, Stephens, Pearce-Higgins, Gregory, & Willis, 2014; Johnston et al., 2015).

The first two chapters of the thesis aims to evaluate the role of protected areas under climate change using long-term data on bird abundancies. These chapters seek to find answers to two main questions:

1) Do protected areas facilitate expansion of the leading range edge of southern species and/or alleviate trailing edge retractions in northern species (**chapter I**)?
2) Does the coverage of protected area networks mitigate climate change driven alterations in bird communities (**chapter II**)?

The white-backed woodpecker (*Dendrocopos leucotos*) is an old-growth deciduous forest specialist, which is dependent on abundant dead wood (Gjerde, Sætersdal, & Nilsen, 2005; Lõhmus, Kinks, & Soon, 2010). It is considered as an umbrella species (Martikainen, Kaila, & Haila, 1998; Roberge, Mikusiński, & Svensson, 2008), the presence of which indicates high forest-bird diversity and the occurrence of endangered polypores and insects (Halme, Mönkkönen, Kotiaho, Ylisirniö, & Markkanen, 2009; Martikainen et al., 1998; Roberge et al., 2008). Therefore, the protection of high-quality habitats for white-backed woodpecker provides shelter also for other endangered species. The white-backed woodpecker has nonetheless suffered from reduced occurrence of forests dominated by deciduous trees and a reduced availability of dead wood, resulting from wide-scale changes in forest structure (Carlson, 2000; Czeszczewik & Walankiewicz, 2006; Garmendia, Cárcamo, & Schwendtner, 2006; Virkkala, Alanko, Laine, & Tiainen, 1993). Northern range margin populations in both Sweden and Finland have been on the brink of

extinction (Laine, 1995; Mild & Stighäll, 2005), but increased since thanks to protection and immigration from Russia (**chapter III**). The aim of **chapter III** is to assess the role of protecting high-quality habitat patches in preventing local extinctions and facilitating colonization events. I do this by studying the unique case of the Finnish white-backed woodpecker population.

Chapter IV concentrates on restoration of degraded wetlands in southern Finland, where also the protected and most valuable wetlands have been encumbered with substantial nutrient loads from human settlements, forestry and agriculture (Ekholm & Mitikka, 2006; Finni, Laurila, & Laakkonen, 2001; Nieminen et al., 2018; Räike et al., 2003). The common reed (*Phragmites australis*) establishes homogenous high-sward populations following eutrophication (Meuleman, Beekman, & Verhoeven, 2002; Zedler & Kercher, 2004). This will lead to the gradual filling of shallow wetlands and result in biodiversity reductions (Meyerson, Saltonstall, Windham, Kiviat, & Findlay, 2000; Zedler & Kercher, 2004). The studied management actions were focused on the most valuable wetlands for waterbirds and were aimed to restore open coastal meadows and areas of open water by counteracting the overgrowth. **Chapter IV** aims to reveal the most effective management actions thwarting overgrowth and enhancing the feeding conditions of both breeding and staging wetland bird guilds. The chapter also evaluates the cost-efficiency of the management actions by assessing the bird guild-specific responses to the funds invested.

3. Methods

3.1 Study area

In studying how climate change and habitat degradation concurrently affect Finnish avian communities, this thesis covers a wide range of species and habitats from breeding land birds in forests and mires to breeding and staging waterbirds and passerines in wetlands. The study area in **chapters I & II** ranges throughout Finland, while **chapter III** covers the whole range of white-backed woodpecker in Finland. **Chapter IV** is restricted to the most valuable wetlands for birds in southernmost Finland. The study areas of all the chapters are presented in Figure 1.

3.2 Data on land bird abundancies

Thanks to a strong basis for citizen science, Finland has a long tradition of bird monitoring and therefore long-term changes in avian abundancies and ranges are well documented even in a global perspective (Lenoir et al., 2019). Starting from the early 1970s line transects have been counted throughout Finland both inside and outside protected areas and coordinated by the Finnish Museum of Natural History and Metsähallitus, National Parks Finland. Originally line transects were located freely in the landscape, fluctuated in length and only quantified the numbers of land birds. In 2006 a new standardized line transect grid was established where transects were placed randomly in the landscape every 25km, set to span 6km and quantifying all bird species and individuals (Väisänen, 2006).

Transects were surveyed yearly during a single visit by walking at a moderate pace (ca. 1km / 45min) (Virkkala & Lehikoinen, 2014). The survey period ranged from the 21st of May to the 20th of June in southern Finland and from the 10th to the 30th of June in northern Finland. In the northernmost montane parts of the country surveying continued until the 5th of July. The differing surveying times at the different latitudes were due to the later onset of spring and thus later breeding of birds at more northern sites. Transects were surveyed in the early morning in weather conditions favourable for detection of birds. All bird individuals were documented and classified according to whether they were singing, calling, flying and/or nesting. In addition, the sex, age and brood and flock-size was recorded when applicable. Based on this information, all observations were transformed into numbers of pairs (e.g. a singing male = 1 pair; **chapter I**). Observations included only individuals which were identified to species level with the exception of crossbill species (*Loxia sp*) which are difficult to distinguish from one another based on the vocalization alone, yet they form a notable part of the observations. The locations of all individuals observed along the transect were documented in either to the main belt spanning 25 meters on both sides of the surveyor or as being located outside this main belt. The ratio of observations inside and outside the 50m wide main belt was calculated based on the data from protected areas in all sections and on both periods for all the studied species. This ratio was used as a species-specific detectability coefficient. The relative density of each species was calculated by multiplying the observed number of pairs per transect kilometre with a species-specific detectability coefficient (Lehikoinen & Virkkala, 2016). The detectability coefficient was used to avoid the

overrepresentation of easily detectable species (e.g. loud and visible species) and the underrepresentation of species difficult to detect (e.g. elusive, small and relatively silent species), which may lead to biased conclusions regarding the composition of the bird community (Johnston et al., 2015). The observed number of pairs, corrected for detectability, were then divided by the transect length to obtain relative densities. Due to the known length of all transects, the counts are corrected for survey effort, which is standardized since 2006.

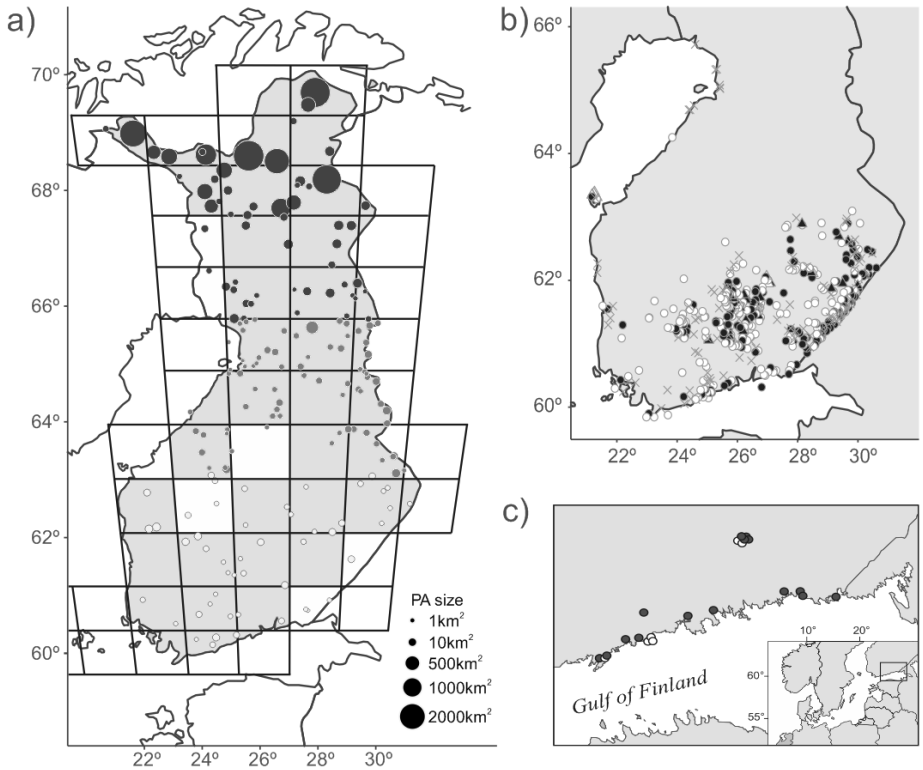

Figure 1. *The study areas of this thesis.* ***a)*** *represents the* ***chapters I & II:*** *Finland was divided into 100kmx100km squares in* ***chapter I*** *and within each square the abundancies of land birds were studied both inside and outside protected areas. In gray filled squares adequate data from both inside and outside protected areas from two time periods (1970s-1980s and 2000s) was available. White squares failed to fulfil this demand. In* ***chapter II,*** *protected areas were studied in three sections of Finland and these sites and their sizes are shown. Light circles represent protected areas in southern, grey circles central and dark circles northern Finland.* ***b)*** *illustrates the territories of white-backed woodpeckers monitored in 2010 (****chapter III****). Triangles represent high-quality patches and circles low-quality patches, while crosses stand for patches of unclassified habitat quality. Dark grey filling represents occupied territories and white unoccupied ones.* ***c)*** *shows the wetlands managed in* ***chapter IV*** *(dark circles) and the unmanaged control sites (white circles).*

The line transect methodology is appropriate for obtaining robust relative abundances of a large set of species over large areas (Järvinen & Väisänen, 1975; Lehikoinen & Virkkala, 2016). By repeating transect lines annually over long periods and large spatial coverage, it is possible to study long-term changes in bird abundances and ranges and link these to environmental alterations such as climate change. The strengths of these data include i) unique long temporal coverage both inside and outside protected areas of a wide set of species, ii) increased reliability of results deriving from abundance rather than occurrence data (Howard et al., 2014; Johnston et al., 2015), iii) known and standardized sampling effort, which also increases reliability, because failing to account for sampling effort can cause biases in results, and increasingly so when occurrence data are used (Kujala, Vepsäläinen, Zuckerberg, & Brommer, 2013).

3.2.1 Bird abundancies at the range edges

In **chapter I**, the change in abundancies of 100 land bird species were studied both inside and outside protected areas between two time periods of 1970–1989 and 2000–2014. The factors affecting bird abundances in the two periods were studied separately for the leading range edge of 70 southern species and for the trailing range edge of 30 northern species. The abundances of each species in each period and a given protection status (protected/unprotected) were pooled within every 100km x 100km square of the country (Fig. 1a).

The range edges of southern and northern species were defined using a percentage of the cumulative density sums in 1970–1989, using data from both inside and outside protected areas (Fig. 2). The densities of all 100km x 100km squares in a latitudinal row of squares were summed and the cumulative density sums of these rows were used when defining the range edge, starting from the southernmost row for southern species and northernmost row for northern species. The edge of the distribution range was defined as starting from the row of squares where the cumulative density sum of the species in question reached at least 95% of the total density of the species. We defined the range edge as continuing from this row until the southernmost latitudinal row for northern species and the northernmost latitudinal row for southern species (Fig. 2).

A protected area reliance index was calculated for each species by dividing the mean density within protected areas by the overall mean density of that species. Range edges were excluded in this calculation to avoid circularity, but both time periods were included in the calculation. The protected area reliance index ranged from 1 to 0 where the extreme values corresponded to all and none of the individuals of the species being observed inside protected areas, respectively. The protected area reliance index was used as a proxy for the importance of protected areas for a given bird species and used for exploring the species-specific role of protected areas in modifying changes in abundance.

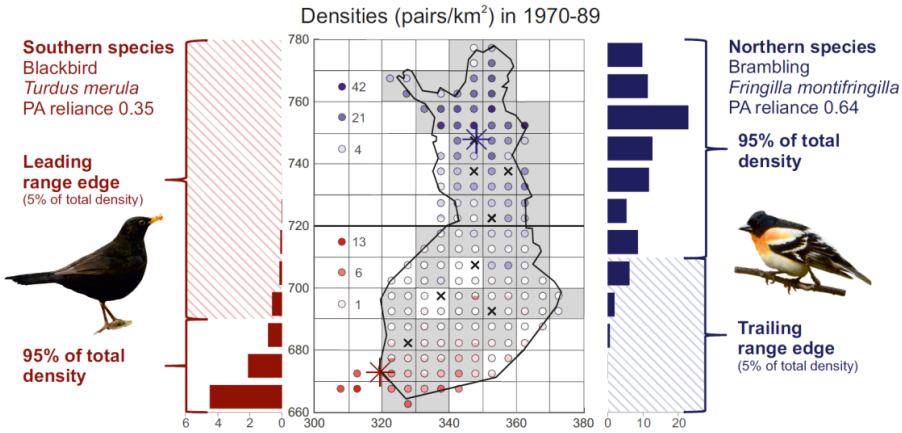

Figure 2. *Definition of range edges of southern (red) and northern species (blue) in **chapter I**. Grey squares represent the spatial coverage of the study (explained in Fig. 1a). Filled dots illustrate densities of species in 1970–1989 inside each 100km x 100km square with a resolution of 50km x 50km. The density of northern species is represented by the upper half of the dot and the density of southern species in the bottom half, where the ranges of the example species overlap. Asterisks represent the central point of gravity of the densities and black crosses missing data. The summed densities of abundances in 100km wide latitudinal zones of squares are shown as histograms on the sides of the map. The range edges (barred areas) represent the southernmost (on northern species; the brambling) or the northernmost (on southern species; the blackbird) 5% of the total density.*

3.2.2 Bird abundancies and community temperature index

In **chapter II**, we studied the effect of protected area coverage on the changes in avian communities within protected areas between the two periods: 1980–1999 and 2000–2015. Community temperature index (hereafter CTI) (Devictor, Julliard, Couvet, & Jiguet, 2008) was used to investigate these climate-driven impacts on biological communities. Climate induced range shifts typically cause decreases in cold-dwelling and increases in warm-dwelling species at a given location (Lenoir et al., 2019), and lead to increased CTI values (Devictor et al., 2012; Santangeli, Rajasärkkä, & Lehikoinen, 2017). In this study we used line transect data from 181protected areas in the country (Fig. 1a).

Relative densities of 171 land bird species encountered on the line transects were used to generate CTI values for each protected area for both time periods separately. The CTI values were generated by first obtaining species temperature index (STI) for each of the 171 species considered. The average temperature of March–August in years 1950–2000 across the breeding range of the species in the whole of Europe was used as the STI (Devictor et al., 2008). The species ranges were obtained from (Hagemeijer & Blair, 1997) and the temperature data from www.worldclim.org. The obtained STIs represent the spatial association of a given species to certain temperatures and are the

basis for generating CTIs (Devictor et al., 2008). The CTIs for both periods within a protected area were calculated by weighting the STIs with the mean annual relative densities of the species present in that period and protected area, and finally averaging across density weighted STIs of all the species (Devictor et al., 2008; Lindström, Green, Paulson, Smith, & Devictor, 2013). Thereby, the CTIs represent a temperature preference of an average individual in the community.

3.3 Data on white-backed woodpecker territories and immigration

Chapter III concentrated on studying the effects of habitat quality and immigration on the probability of a suitable habitat patch being occupied by white-backed woodpeckers. The breeding site monitoring of this species was coordinated by WWF Finland in 1987–2002 and by Metsähallitus, National Parks Finland since 2003. Most of the sites have been visited annually to record occupancy and breeding success. The study period of **chapter III** ranged from 1991 to 2010, during which the number of monitored sites nearly doubled from 276 to 518. Only the territories monitored since 1991 were included in the study. Monitored sites were visited during early spring corresponding the active displaying period of the white-backed woodpecker. Occupied territories were visited later in order to find nests and record breeding success. The majority of study sites (98%, n = 271) were classified as either high- or lower quality patches. High-quality patches (n = 33) consisted of large uniform patches of open and light old-growth birch forest with abundant dead wood, sparse shrub layer and a close proximity to water or moist land. Lower quality sites (n = 238) were smaller, more fragmented and consisted of young forest. The classification is somewhat subjective, however all sites were classified by a single person expert in the biology and habitat requirements of the white-backed woodpecker.

The immigration intensity of white-backed woodpeckers was studied using migration data obtained from South Karelia on the eastern border of Finland (data of ornithological society of South Karelia, Kontiokorpi 2007b) and Hanko Bird Observatory in southwestern Finland (Lehikoinen et al. 2008). All white-backed woodpeckers passing the South Karelia observation site in flight during autumn, were classified as migrants. All individuals seen at Hanko Bird Observatory were deemed migrants since white-backed woodpeckers do not breed in that area. The annual numbers of migrating woodpeckers at the two sites showed fairly strong positive correlation ($r_s = 0.52$, df = 28, P = 0.003), and the two datasets were used to represent immigration intensity during the years 1991–2010.

3.4 Data on waterbirds and wetland management

During the years 2003–2012 management actions were undertaken with the aim to reduce eutrophication driven overgrowth and restore both coastal meadows and open bodies of water (**chapter IV**, Fig. 1c). Management was conducted in two periods: the first in 2004–2006 and the second in 2007–2012. At 13 sites the management actions were continued into the second

period, while management ceased on the rest in 2006. Each managed wetland was divided into managed and unmanaged sections. The management actions were rather small-scaled and targeted to wetland areas were historically had been open meadows or larger open water areas. For mainly practical reasons, the managed sections of the wetlands were defined as the area spanning a 500m radius from the edge of the actual managed area. The area outside this radius was considered as the unmanaged section of the wetland. If an unmanaged section of water on a single wetland was split by land it was considered as two separate sections. This resulted in a total of 35 wetland sections out of which 17 were managed in the first, and 13 in the second management period.

Birds on the wetlands were counted before management actions took place and the counts were repeated after both management periods. The location of all birds was documented as either on the managed or on the unmanaged sections of the wetland. Visits to count for staging birds were done approximately once every five days and continued throughout the autumn migration season of 2003 and the spring season of 2004. Birds were again counted after the periods of management (autumns 2006 and 2012 and springs 2007 and 2012) in order to evaluate the effect of the management actions on the number of staging birds. Breeding birds were censused in April–June 2004 and 2007, either by counting pairs from pre-set observation points in late April or early May and repeated at the end of May or by mapping territories by walking through the whole wetland once every two weeks in May–June. Each active territory was counted as one breeding pair. Species-specific bird numbers in each season on each wetland section were grouped into ten guilds based on foraging behaviour and breeding habitat preferences: (i) dabbling ducks, (ii) diving omnivores, (iii) diving piscivores, (iv) swans, (v) geese, (vi) waders, (vii) black-headed gull, (viii) rallids and bittern, (ix) open habitat passerines, and (x) shrub and reed bed passerines.

The management actions implemented were those commonly used for restoring open habitats (Ausden, 2007) and included: i) mechanical cutting and harrowing of reed beds, ii) cattle grazing, iii) tree and shrub removal and iv) dredging of both impenetrable submerged and emergent aquatic vegetation as well as bottom sediment. The total costs of the management actions at each site were used to study the cost-efficiency of wetland management. Altogether 1.75 M€ were spent on management, with 1.08 M€ and 0.68 M€ during the first and second management periods, respectively. The salaries of administrative or bird counting personnel were not included nor taken into account.

3.5 Statistical analyses

In the thesis frequentist statistical analyses were performed by using program R (R_Core_Development_Team, 2019). In **chapters II & IV** the responses under study were expected to be linear and therefore the analyses used were linear regressions where the residuals adhered to the assumption of normal distribution (change in CTI and number of waterbirds/visit in **chapters II & IV**, respectively). When analyzing count data (pair counts including zeros in

chapter I) generalized linear regressions with Poisson distribution was expected to allow for deviations from normally distributed response. Considerable amount of zero counts caused overdispersion of model residuals observed with Poisson distribution, and therefore negative binomial distribution was implemented instead. To account for the lack of independence and potential pseudoreplication arising from repeated observations, mixed models were implemented (**chapters I, IV**). In **chapter III** the response variable was the probability of observing an occupied territory, a pair or a nest of white-backed woodpeckers and we therefore implemented a logistic regression model.

In cases where we used model sets for inference, the models were ranked according to their Akaike Information Criterion (AIC) value (Akaike, 1974). If several models performed equally well, model averaging was implemented (**chapters I, II & III**) (Arnold, 2010). In **chapter IV**, we implemented a stepwise reduction of uninformative variables, resulting in all remaining variables, in addition to fixed variables, showed statistical significance. When applicable, the residuals of our models were inspected for potential spatial autocorrelation, and/or unexplained patterns (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), however none were detected.

4. Results and discussion

4.1 The effect of protected areas on changes at the range edges

Abundances of northern species at the trailing edge of their range were higher inside protected areas (Fig. 3, **chapter I**). Bird abundances decreased with increasing protected area reliance, but an interaction between protection status and protected area reliance indicated that the decrease was much steeper outside protected areas than inside them (Fig. 3a). Moreover, the abundances of northern species on the trailing edge of their range declined from the 1970s–80s to the 2000s, but the decrease was less marked inside protected areas than it was outside (Fig. 3b). Especially species with high protected area reliance exhibited higher abundancies in protected areas compared to those outside them. While this was partly expected due to a generally higher reliance on protected areas among northern species (mean protected area reliance 0.63 ± 0.14 SD), it underlines the fact that species with the highest reliance on protection were nearly absent outside protected areas in the 2000s. These differences could be explained by the high proportion of high quality old-growth boreal forests inside Finnish protected areas, and the striking lack of these habitats outside protected areas. A high prevalence of old growth forest has been shown to have a positive effect on the degree of specialization of the avian community (Häkkilä et al., 2017).

These results underline the importance of protected areas in mitigating declines of boreal bird species under climate change. The velocity of climate change in the boreal biome protected areas is predicted to be much faster than that in protected areas in other biomes, carrying serious consequences for ecosystems and associated wildlife (Loarie et al., 2009). Despite the fact that northern protected areas are experiencing the shortest climate residence times (Loarie et al., 2009), these protected areas are still able to delay the retraction of species ranges. These findings support the previously reported importance of protected areas have in mitigating the negative effects of climate change by aiding the persistence of northern species (Gillingham, Alison, Roy, Fox, & Thomas, 2015), facilitating the adaptation of northern species to temperature changes (Gaüzère, Jiguet, & Devictor, 2016) and supporting more cold-adapted bird communities (Santangeli et al., 2017).

In contrast to northern species, the abundances of southern species at the leading edge of their range were higher and increased more outside than inside protected areas during the study period (Fig. 3). However, inside protected areas bird abundances increased markedly with increasing protected area reliance index (Fig. 3c), whereas outside protected areas these reliance indices showed no statistically significant effect on bird abundancies (**chapter I**). Protected area reliance interacted positively with time period, showing that bird abundances increased with increasing protected area reliance from the 1970s–80s to the 2000s (Fig. 3d). Abundances of southern species on the leading edge of their range showed an overall increase from the 1970s–80s to the 2000s, however, this increase was not as marked inside protected areas as outside (Fig. 3d). The protected area reliance was low in southern species (mean 0.39 ± 0.19 SD), and species highly reliant on protected areas showed markedly higher abundancies inside protected areas

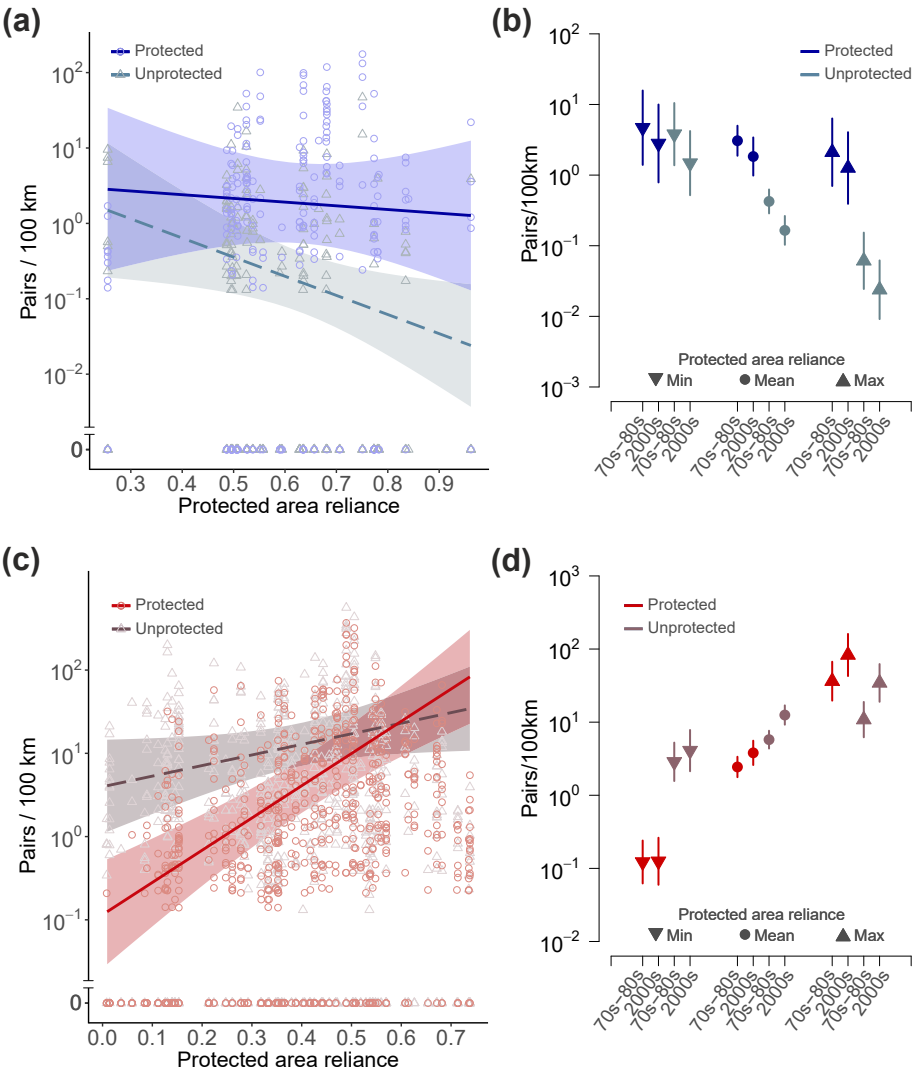

Figure 3. *Model estimates of bird abundance in response to protected area reliance and time period.* ***a)*** *and* ***c)*** *show the estimated effects of protected area reliance on bird abundances inside protected areas (solid line) and outside protected areas (dashed line) during the second time period (2000s) of northern species and southern species, respectively; circles represent data points from protected areas and triangles those from unprotected areas. Shaded bands represent the 95% confidence intervals of the effect of protected area reliance on bird abundance.* ***b)*** *shows model estimates of the effect of time period on densities of northern species (inside protected areas: dark blue, outside protected areas: light blue) for minimum (0.25; point-down triangles), mean (0.63; dots) and maximum (0.96; point-up triangles) protected area reliances.* ***d)*** *shows model estimates of the effect of time period on densities of southern species (inside protected areas: red, outside protected areas: dark pink) for minimum (0.01; point-down triangles), mean (0.39; dots) and maximum (0.74; point-up triangles) protected area reliance indices.*

than outside (Fig. 3d). This suggests that protected areas are important for expansions of species reliant on protected areas, which has also been established by studies on birds, butterflies and odonates in a more southern temperate region (Gillingham, Alison, et al., 2015; Gillingham, Bradbury, et al., 2015). Thus, it is clear that protected areas can act as stepping stones for species with high protected area reliance when colonizing new areas (Hiley, Bradbury, Holling, & Thomas, 2013).

For southern species increasing protected area reliance had a positive effect on bird abundancies also outside protected areas in the 2000s, as compared to the 1970s–80s. This may be the result of protected area designation being biased towards boreal habitats. Therefore, if species with high protected area reliance had positive associations with boreal habitats, they could find suitable habitat outside protected areas when expanding their distributions from the temperate zone into the boreal zone. This could pose a challenge for national conservation under climate change. Current protected area networks maintaining habitat for northern species could need extensions and management to provide habitat important also for the northward expansion of southern species, some of which might not have existed in Finland before. National protected area networks show higher connectivity than continental networks, wherefore more focus in needed on increasing the coverage of protected area networks on a continental scale (Santini, Saura, & Rondinini, 2016).

4.2 The effects of protected area coverage on changes in avian communities

The CTI-values of bird communities inhabiting protected areas in northern and central Finland showed lesser change between the study periods (1980–1999 and 2000–2015) the higher the protected area coverage was within a 100km radius (Fig. 4). In southern Finland such an association was not detected.

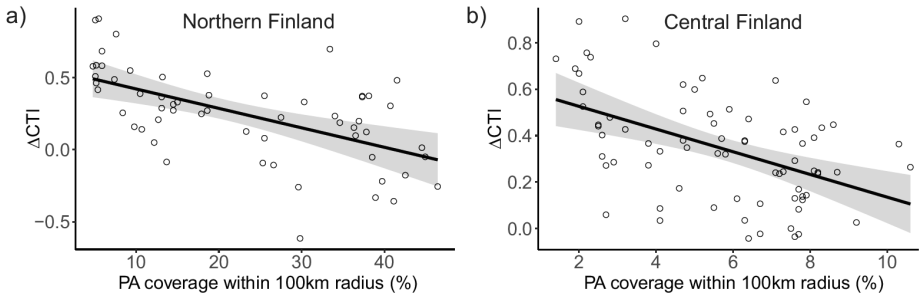

Figure 4. *Model estimates of the effects of protected area coverage on community temperature index changes (ΔCTI) within protected areas between the two periods of 1980–1999 and 2000–2015 in **a)** northern Finland and **b)** central Finland. The solid line represents the estimated effect of protected area coverage within 100km radius on the ΔCTI, and the grey band represents the 95% confidence interval of this effect. Circles represent the partial residuals of observed values.*

These results show that increasing protected area coverage within a 100km radius indeed mitigated climate-driven community changes in protected areas. Although CTIs have increased also within the protected areas, a previous study shows that communities within Finnish protected areas exhibit higher densities of cold-dwelling species than neighbouring unprotected areas (Santangeli et al., 2017) The CTI-values of the avian communities within protected areas are still lower than those observed outside protected areas in the 1970s–1980s (Santangeli et al., 2017). In **chapter I** of this thesis I show that the abundances of cold-dwelling bird species at the trailing range margins are higher inside protected areas than outside them, a pattern also observed in the UK (Gillingham, Bradbury, et al., 2015). Protected areas are shown to facilitate the adaptation of high latitude species to a warming climate (Gaüzère et al., 2016), and even though the abundancies of cold-dwelling northern species have declined inside Finnish protected areas (Virkkala & Rajasärkkä, 2011); **chapter I**), these studies strongly indicate an important role of protected areas in aiding the persistence of diverse cold-dwelling species assemblies. The results of **chapter II** additionally suggest that the ability of protected areas to fulfil this role is further improved by an increased proportion of protected areas in the landscape. Support for the notion that increased protected area coverage facilitates the persistence of avian communities arises from the African Savannahs. Beale, Baker, Brewer, and Lennon (2013) show that climatic conditions drive bird species to colonize new areas and such colonization events are more frequent with increasing protected area coverage, while local extinctions, in turn, are less frequent the higher the protected area coverage is. Correspondingly, a Finnish study has revealed that increased proportions of old-growth boreal forests in the landscape matrix surrounding protected areas are positively associated with the specialization of avian communities within the protected areas, suggesting that protected areas surrounded by intense forestry are not able to maintain their species assemblage and levels of species abundances (Häkkilä et al., 2017).

We found no effect of protected area coverage on community changes in southern Finland, where the protected area coverage is clearly the lowest among the three studied sections of the country (Fig. 1, **chapter II**). The network of protected area in southern Finland may be too fragmented to support detectable levels of community resilience against climate change.

The projected occurrence hotspots of forest bird species in Finland have shown weak relation to protection, especially in southern Finland (Virkkala, Heikkinen, Fronzek, & Leikola, 2013). This was explained with the very low extent of protected forest cover of 2.3% and 3.7% in southern and middle boreal zones in Finland, respectively, compared to 23% of protected forests in the northern boreal zone (Virkkala et al., 2013). Another recent study showed that avian densities inside Finnish protected areas had declined since the year 1980 in southern, but not in northern Finland (Virkkala et al., 2018).

Populations and communities are more resilient to environmental changes when the landscape matrix contains a higher proportion of suitable high quality habitat (Hanski, 1998; Hodgson, Moilanen, Wintle, & Thomas, 2011). Due to the exclusion of land development and forest management from Finnish protected areas, these areas support older, more layered forest and higher

volumes of dead wood than unprotected forests (Metsähallitus, 2019). Pristine forest mires are rare outside protected areas, since c. 60% of the original mires have been drained by ditching for forestry purposes (Fraixedas et al., 2017). Thus, habitat quality could indeed explain the observed differences between unprotected and protected areas in the persistence of communities and populations.

4.3 The effect of habitat quality on patch occupancy

The frequency by which occupied territories, pairs and confirmed breeding records of white-backed woodpeckers were detected increased throughout the period spanning from 1991 to 2010 (Fig. 5), and was largely the result of a strong increase in population size (**chapter III**). These observation frequencies were markedly higher and seemed to have increased more steeply at high quality than at lower quality sites (Fig. 5); thereby high quality habitats were more frequently inhabited and produced young more frequently than lower quality sites. The increase in observation frequency was more marked in the eastern parts of the study area (**chapter III**). This is partly is expected since immigration mainly occurs from the east in this species in Finland, and since higher immigration intensity clearly improved the probability of observing occupied territories and paired white-backed woodpeckers (**chapter III**). The increased frequency of site occupancy in high quality habitats could mean that these sites are preferentially colonized by migrants. However, the increase in observation frequency was also present in all models including irruptive migration, suggesting that the increase was at least partly independent of immigration. The increased frequency of occupancy at high quality sites could thereby also be explained partly if these sites were abandoned less frequently than lower quality sites.

Annual mean breeding success (chicks/confirmed breeding) increased significantly during 1991–2010, and did not differ between high and lower quality sites (**chapter III**). However, considering that successful breeding was much more frequent at high quality sites than lower quality ones, these sites produced more potential recruits to the population than the lower quality sites. It is thus possible that the high quality sites served as sources for the white-backed woodpecker population during the increase.

These results suggest that high quality sites have been more effective than lower quality sites in preserving the Finnish white-backed woodpecker population. Most of the high quality sites were protected when the white-backed woodpecker population was at its lowest, thus guaranteeing the existence of direly needed high quality habitat.

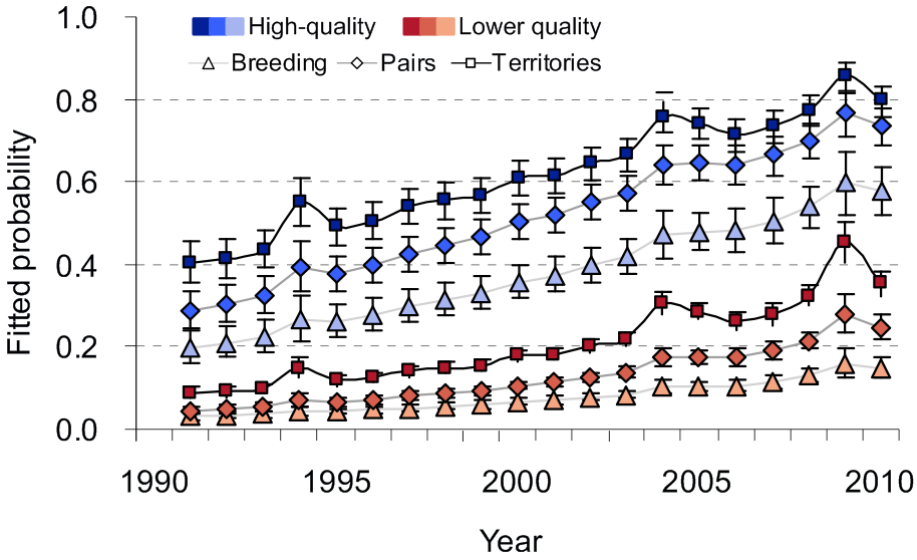

Figure 5. *Model predictions of the probabilities of detecting white-backed woodpecker nests, pairs and territories at sites in high quality (blue) and lower quality (red) habitat. The whiskers represent 95% confidence intervals.*

4.4 Management and restoration for increasing habitat quality

Unfortunately, protection *per se* has not been sufficient enough to preserve high quality habitats in Finnish wetlands, which have become severely eutrophicated and overgrown. Although the wetlands themselves may have been protected, the protection status did not prevent a considerable anthropogenic nutrient load, derived from e.g. forestry and agriculture from entering the wetlands (Ekholm & Mitikka, 2006; Finni et al., 2001; Nieminen et al., 2018; Räike et al., 2003). The wetland habitats quality could, nonetheless, be improved by thwarting overgrowth and thereby inducing a positive response in the numbers of breeding and staging birds (**chapter IV**). Cattle grazing increased the numbers of breeding and spring staging birds of all guilds, and showed positive associations with dabbling ducks, swans, waders and black-headed gull during the autumn migration (Table 1, Fig. 6). Grazing was also the only management action that increased the number of staging birds belonging to species red-listed by the EU and to species listed in the Bird Directive Annex I during both the spring and autumn migrations. Mechanic cutting of reed beds showed a positive association with the number of staging dabbling ducks and waders in spring, and EU red-listed species in autumn. Dredging in turn increased the numbers of staging waders and black-headed gulls in spring and red-listed species in autumn. Dredging also increased the number of breeding black-headed gulls, rallids and bittern. However, dredging was the only management action having a negative effect on waterbirds, whereby it decreased the numbers of piscivores both during the breeding and the spring staging periods. This is most likely due to increased turbidity caused

by dredging, which may hamper the feeding efficiency of these visual predators preferring wetlands with clearer water (Eriksson, 1985). Against our predictions, grazing and cutting did not show a negative association with the number of breeding reed bed passerines, although these actions markedly reduced the extent of their breeding habitat. This could be explained by increased food abundance in the cut reed bed (Poulin & Lefebvre, 2002) and by a sufficient amount of breeding habitat still being left after the management actions.

The invested funds were in general positively correlated with the number of birds frequenting the wetlands (Table 1, Fig.6). This suggests that invested funds facilitate habitat improvement and thereby increase the number of waterbirds. From both conservation and socioeconomic point-of-views it is reassuring that the amount of funds invested in wetland management was not only positively correlated with the abundance of common species, but also with that of red-listed species (Table 1). The number of breeding diving piscivores, however, showed a negative association with the invested funds. This is most likely the effect of dredging, which is expensive and may impair feeding efficiency of piscivores due to increased turbidity (Eriksson, 1985).

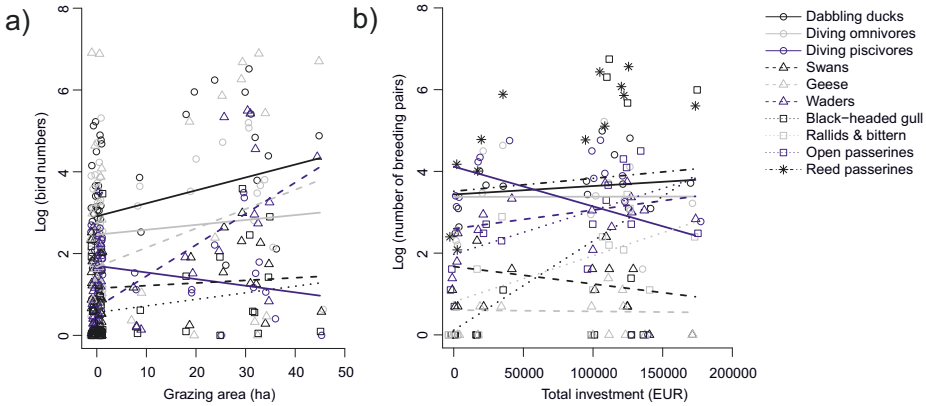

Figure 6. *Examples of the effects of the guild specific responses to management actions and invested funds.* ***a)*** *shows the responses of staging spring migrant birds to the extent of grazed area; dabbling ducks, geese and waders showed statistically significant positive response to the extent of grazing area.* ***b)*** *illustrates responses of breeding birds to the total funds invested in management; black-headed gull, rallids and bittern as well as open area passerines exhibited statistically significant positive associations, whereas diving piscivores showed a significant negative association with the amount of invested funds.*

These results show that management was associated with a rapid increase in waterbird numbers on the studied wetlands. Importantly, bird abundances in every guild showed a positive correlation with one or more management actions and all actions, except shrub and tree removal, were positively

associated with the bird numbers of at least one guild. Grazing showed more positive associations than any other management action, which underlines the central role of livestock grazing in the preservation of ecological diversity in open habitats (Vickery et al., 2001). By creating a mosaic of vegetation of different length and structure and by providing dung, cattle increase the biodiversity of grassland plants and invertebrates (Dittrich & Helden, 2012; Hart, 2001; Møller, 2001), which, in turn, improves the abundance and species richness of birds (Lengyel, Deri, & Magura, 2016; Mérő et al., 2015; Voslamber & Vulink, 2010).

We also show that wetland management can mitigate the negative effects of eutrophication-induced common reed overgrowth. This is both an important and a highly useful finding, since eutrophication-induced overgrowth and biodiversity loss due to plant invasions are worldwide problems (Davis, Grime, & Thompson, 2000; Downing, 2014), and these actions could be applied to thwart reduces in biodiversity and bird abundance (Meyer, Badzinski, Petrie, & Ankney, 2010; Zedler & Kercher, 2004). The fact that waterbird species are threatened by ongoing eutrophication and overgrowth (Lehikoinen et al., 2016; Tiainen et al., 2016) and have become increasingly red-listed in Europe (BirdLife_International, 2015), further underlines the importance of elucidating ways to mitigate these negative developments. Recent climate change emphasizes the importance of effective management actions, because climate change induced increases in precipitation are suggested to increase the nutrient flow into boreal wetlands in Europe (Meier et al., 2012) thus potentially exacerbating current eutrophication and overgrowth related problems. At the same time many waterfowl species have markedly delayed their autumn migration (Lehikoinen & Jaatinen, 2012) and shifted their wintering areas to higher latitudes due to climate change (Lehikoinen et al., 2013; Pavon-Jordan et al., 2015), meaning that the importance of these northern wetlands as waterfowl staging and wintering areas will increase markedly.

Table 1. *Model estimates of the effects of wetland management actions and invested funds on staging and breeding bird guilds as well as species on the EU red-list and in the Bird Directive Annex I. The estimates represent the effect of one hectare of management on log(staging individuals/visit) in autumn and spring and log(pairs/wetland) during the breeding period. For the invested funds the estimate represents the effect of 1000 euros for log(staging individuals/visit) in autumn and spring and log(pairs/wetland) during the breeding period. Statistically significant effects are bolded and trend indicating effects are marked with asterisk (*). Management actions showing no statistically significant effects in a given season are marked with hyphen (-) and those where data was not available are marked with "n/a".*

	Cutting			Grazing			Dredging			Invested funds		
Guilds	Autumn	Spring	Breeding	Autumn	Spring	Breeding	Autumn	Spring	Breeding	Autumn	Spring	Breeding
Dabbling ducks	-	**0.02**	-	**0.04**	**0.05**	**0.02**	-	0.03	0.00	**0.01**	**0.01**	0.00
Diving omnivores	-	-0.01	-	0.02	**0.05**	**0.02**	-	0.01	0.01	0.00	-0.00	0.00
Diving piscivores	-	-0.01	-	-0.00	**0.05**	**0.02**	-	**-0.06**	**-0.05**	-0.00	0.00	**-0.01**
Geese	-	-0.01	-	0.02	**0.05**	**0.02**	-	0.01	-0.01	**0.02**	**0.01**	0.00
Swans	-	0.00	-	**0.06**	**0.05**	**0.02**	-	0.02	0.02	0.00	0.00	-0.00
Waders	-	**0.07**	-	**0.09**	**0.05**	**0.02**	-	**0.08**	0.02	**0.02**	**0.02**	0.00
Black-headed gull	-	0.02	-	**0.03**	**0.05**	**0.02**	-	**0.05**	**0.06**	**0.01**	**0.01**	**0.02**
Rallids & bittern	n/a	n/a	-	n/a	n/a	**0.02**	n/a	n/a	**0.07**	n/a	n/a	**0.01**
Open area passerines	n/a	n/a	-	n/a	n/a	**0.02**	n/a	n/a	0.01	n/a	n/a	**0.01**
Reed passerines	n/a	n/a	-	n/a	n/a	**0.02**	n/a	n/a	0.04	n/a	n/a	0.00
EU Red List	**0.03**	-	n/a	**0.03**	**0.06**	n/a	**0.04**	-	n/a	**0.01**	0.01*	n/a
Bird Directive Annex I	-	-	n/a	**0.03**	**0.03**	n/a	-	-	n/a	-	-	n/a

5. Conclusions

The main result of this thesis is that climate change driven range and community changes can be mitigated by conserving a high coverage of high-quality natural habitats (**chapters I, II, III, IV**). It supports the projections that improvement of multispecies connectivity could be reached by increasing protected area size and coverage in the landscape (**chapter I)** (Santini et al., 2016), especially so when the habitats within protected areas are managed (**chapter IV**) (Lawson et al., 2014). Bird populations are shifting northwards (Lehikoinen & Virkkala, 2016) and this occurs also in protected areas (**chapters I, II, III**) (Virkkala et al., 2018) despite their mitigating effect on range shifts in northern species. Although protected areas play an essential role in supporting species in adapting to global warming, and thus conserve biodiversity by facilitating range expansions (Gillingham, Alison, et al., 2015; Johnston et al., 2013; Thomas et al., 2012), communities residing at high latitudes and altitudes are unable to retreat ceaselessly (Pacifici et al., 2017). Therefore, northern protected areas are projected to become increasingly important refuges for biodiversity under climate change (**chapters I, II)** (Berteaux et al., 2018), and thus preserving high quality natural and semi-natural habitats should become the main focus of conservation actions (Hodgson, Moilanen, et al., 2011). Comprehensive protected area networks at high latitudes and altitudes could markedly increase the climate resilience by allowing time for adaptation (**chapters I, II)** (Keeley et al., 2018).

Unfortunately, the present conservation efforts seem to be insufficient for preventing biodiversity loss (Butchart et al., 2010), and aims to conserve and manage natural resources cannot be met on the current trajectories (IPBES, 2019). Therefore, further expansions of protected area networks are direly needed (CBD, 2018; Montesino Pouzols et al., 2014) in order to provision sufficient geographic and temporal coverage and so aid declining species and changing communities (Runge et al., 2015). The international Aichi Target 11 (CBD, 2018) aims to tackle the ongoing loss of biodiversity by increasing the amount of well-connected protected land coverage worldwide so that it reaches 17% by 2020. Currently there are remarkable global differences in the coverage of protected areas, and alarmingly, only 7.5% of the global land mass is covered by well-connected protected areas (Saura, Bastin, Battistella, Mandrici, & Dubois, 2017). This notion and the main conclusion of this thesis emphasize both the need for extensive and rapid efforts to increase protected area coverage and connectivity globally (Saura et al., 2018), and the benefits this will have for preserving biodiversity for coming generations.

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